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PARTICLE SIZE AND FLOW VELOCITY INDUCE AN INFERRED SWITCH IN BRYOZOAN SUSPENSION-FEEDING BEHAVIOR

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ABSTRACT

The feeding rates of two bryozoan species varied with particle size and flow velocity. In one species, increased flow reduced feeding on larger particles. The anomalously high capture rate of the largest particles by the smaller of the two species indicates a switch in feeding by ciliary currents to feeding that involves a high degree of tentacular activity. This is the first quantification of feeding under alternate modes in a benthic invertebrate and suggests that tentacular feeding may provide a significant source of nutrition for bryozoans.

INTRODUCTION

It is increasingly clear that switches in feeding strategies are common in benthic marine organisms. Some polychaetes, clams, and amphipods switch from deposit to suspension feeding with increases in flow or suspended material; some corals both entrap zooplankters with their tentacles and use mucus to entangle suspended particles; and some active suspension feeders feed passively under certain conditions (*e.g.*, barnacles, ascidians, brachiopods, and sponges) (Lewis and Price, 1975; Taghon *et al.*, 1980; Dauer *et al.*, 1981; LaBarbera, 1984; Ólafsson, 1986). There is also evidence for alternate feeding modes in zooplanktonic suspension feeders. Copepods have been argued to filter feed on small particles and to actively grasp particles of larger size (*e.g.*, Conover, 1966; Richman and Rogers, 1969; Poulet, 1974) [but see more recent clarification of copepod feeding by Koehl and Strickler (1981)]. In addition, many suspension feeders take up dissolved organic matter, although the process is presumably continuous and would entail no switch in feeding behavior (Stephens and Schinske, 1961; Jørgensen, 1976; DeBurgh and Fankboner, 1978; Stewart, 1979).

In bryozoans, feeding currents produced by cilia lining the tentacles of the lophophore can be accompanied by a high degree of tentacular activity ranging from simple individual tentacle-flicking to encaging particles with all of the tentacles (Winston, 1978). Encagement activity is generally observed when particles are large; however, there has been no explicit test of the factors promoting greater tentacular *versus* ciliary feeding in bryozoans. In addition, the amount of food ingested under alternate modes has not been determined for any benthic invertebrate. This study compares the effects of particle size and ambient flow velocity on the feeding of the two closely related arborescent bryozoans, *Bugula neritina* and *B. stolonifera*.

Bryozoans are exclusively colonial animals common in both modern and fossil marine habitats. A variety of colony morphologies are found among bryozoan spe-

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TABLE I

Dimensions[1] *of* Bugula neritina *and* B. stolonifera

	Bugula neritina	*Bugula stolonifera*
Maximum size of colony (cm)	8	3–4
Number of tentacles	23–24	13–14
Mean length of tentacles (cm)	6.16×10^{-2}	4.47×10^{-2}
Mean diameter of lophophore (cm)	7.64×10^{-2}	4.41×10^{-2}
Mean diameter of mouth (cm)	7.4×10^{-3}	4.9×10^{-3}

[1] Values from Ryland and Hayward (1977) and Winston (1978, 1982).

cies. These include encrusting, arborescent, and massive colonies. The zooids (modules) that compose bryozoan colonies also vary substantially in form and function both among species and within colonies of the same species. Feeding zooids ingest suspended particles using the ciliated crown of tentacles, the lophophore. Gut contents and laboratory rearing experiments indicate that flagellates and diatoms can be important food items (Winston, 1977, and references therein). However, little is known of the food sources for field populations since plankton is inherently patchy in nature, the partial digestion of gut contents hinders identification of ingested material, and the small size of feeding zooids and the even smaller size of their prey make direct observation in the field difficult. The effect of flow on bryozoan feeding has received some attention (Okamura, 1984, 1985), but the effect of particle size is unknown.

MATERIALS AND METHODS

Colonies of the arborescent, anascan cheilostomes *Bugula stolonifera* and *B. neritina* co-occur in fouling communities that develop on submerged structures in ports and harbors. In Florida, colonies occur on seagrasses, oyster shells, docks, canal walls, floats, rotting wood, algae, coastal rock ledges, and inlet breakwaters (Winston, 1982). Both species are widespread. *B. stolonifera* is the smaller species (see Table I) and often colonizes and grows within *B. neritina* colonies. In this study, *B. neritina* and *B. stolonifera* colonies were collected from the floating docks of the Harbor Branch Oceanographic Institution at Link Port, Florida. Laboratory observations of bryozoan feeding behavior confirm that high degrees of tentacular activity and encagement of particles occur in several *Bugula* species (including *B. neritina*) and seem to be associated with particle size and motility (Winston, 1978). However, these observations were made in still water.

Feeding experiments were performed by submerging colonies in a recirculating flow tank (Vogel and LaBarbera, 1978) in which currents of known mean velocities could be created in the working section (13 cm × 13 cm × 13 cm). The flow tank contained a suspension of latex particles (polystyrene divinylbenzene calibration particles: Duke Scientific Corporation, Palo Alto, CA). (Initial observations showed that the bryozoans would ingest these particles.) Two flow velocities were created in the flow tank: a relatively slow flow (1–2 cm/s) and a relatively fast flow (10–12 cm/s). Flow measurements taken with an electromagnetic flow probe (Marsh McBirney No. 523) in the field at the branch tip level of *Bugula stolonifera* (Okamura, 1984) indicate that both species encounter flow velocities in the experimental range (measurements were made in a habitat where both species occurred). Feeding on three sizes of latex particles was assessed at each flow velocity. Particle diameters were 9.6 (SD = 0.5), 14.6 (SD = 1.0), and 19.1 (SD = 1.1) microns. At the outset of experiments, particle concentrations in the flow tank were set at 100 particles/ml by adding appropriate volumes of stock suspensions of known concentrations to a known volume of filtered seawater in the flow tank. Concentrations of 100 particles/ml lie well within the range of concentrations of flagellates measured in the field (*e.g.*, Jørgensen, 1966; Bullivant, 1968). Control runs in the flow tank indicated that latex particles do not settle out of suspension over time at either flow velocity employed (Okamura, 1984).

Up to three replicate colonies were placed in the flow tank during a given experiment. Only portions of colonies were used in all experiments. [Clipping colonies does not affect feeding activity (Okamura, 1984)]. Colonies were allowed to feed for 20 min and then were removed from the flow tank and placed in dilute sodium hypochlorite. This treatment dissolves the organic contents of colonies but leaves intact the exoskeleton, membranous material, and latex particles. Ingested latex particles (that can initially be discerned only poorly in the gut before the gut wall dissolves) remain trapped within the zooidal exoskeleton and membranes and can be counted easily. These counts provided an estimate of the mean number of particles ingested per feeding zooid per colony (range of zooids sampled per colony = 5–100, mean = 64.4, SD = 35.2) (range of colonies replicated per treatment = 8–16). The effects of flow velocity and particle size on the mean number of particles ingested per zooid per colony were then analyzed with two-way analyses of variance for each species.

RESULTS

Bugula neritina ingested few small particles at both flow velocities (see Fig. 1A). More large particles were consumed than medium-sized particles in slow flow. This pattern reversed itself in fast flow (note the nearly significant interaction term). The smaller *B. stolonifera* showed greatest ingestion of medium-sized particles in slow flow (see Fig. 1B). Feeding on medium-sized and small particles was inhibited in fast flow; however, large particles were captured in great numbers.

DISCUSSION

Feeding patterns and their causal explanations

Rubenstein and Koehl (1977) used aerosol models of filtration to clarify suspension-feeding mechanisms, however these models can only be applied to passive suspension feeders. Because bryozoans and other active suspension feeders generate feeding currents, complex three-dimensional flow patterns arise between self-generated feeding currents and local currents near the feeding structures (Jørgensen, 1980). For feeding to occur, particles must be transferred from local currents into the self-generated feeding currents, and in doing so they must pass through a boundary zone characterized by steep velocity gradients (Jørgensen, 1980). The behavior of particles that enter steep velocity gradients is uncertain (Strathmann, 1982). With this in mind, several factors may explain the patterns of feeding from different flows on particles of varying size by *Bugula stolonifera* and *B. neritina*.

Large-sized particles travel with greater momentum and thus may be carried further downstream before crossing flow lines in velocity gradients. Strathmann (1971, 1982) argued that no evidence indicates that momentum carries particles across flow lines so that they will impinge upon the ciliary tracts of echinoderm larvae and lopho-

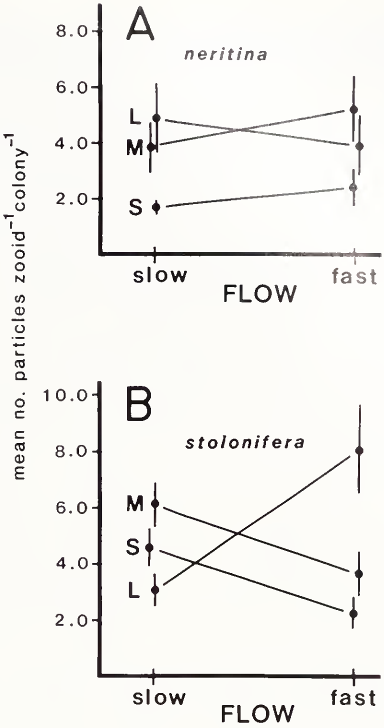

FIGURE 1. Mean number of 9.6 (S), 14.6 (M), and 19.1 (L) micron particles captured per feeding zooid per colony (±2 SE) by *Bugula neritina* (A) and *B. stolonifera* (B) in slow and fast flow. Two-way analysis of variance for *B. neritina:* $F_{1,55}$ (velocity term) = 1.347, $P = 0.251$; $F_{2,55}$ (particle size term) = 18.120, $P < 0.001$; $F_{2,55}$ (velocity × particle size interaction) = 2.931, $P = 0.062$. Two-way analysis of variance for *B. stolonifera:* $F_{1,59}$ (velocity term) = 0.035, $P = 0.0851$; $F_{2,59}$ (particle size term) = 11.183, $P < 0.001$; $F_{2,59}$ (velocity × particle size interaction) = 42.679, $P < 0.001$.

phorates, and hence that momentum does not play a role in the suspension feeding of these organisms. However, the role of momentum in the transport of particles out of local currents and into feeding currents is unknown. Alternatively, the relatively greater drag experienced by large-sized particles may act to sweep them further downstream before crossing flow lines in velocity gradients. Both momentum and drag increase with ambient flow velocity.

The larger lophophores of *Bugula neritina* create stronger feeding currents, and these may account for its greater effectiveness in capturing large particles from slow flow. For *B. stolonifera,* highest ingestion rates in slow flow were on medium-sized particles. In fast flow, *B. neritina* was hindered in feeding on large particles and showed highest ingestion rates on intermediate-sized particles. The greater momentum of or drag on large particles in faster flow may make their ingestion more difficult. However, anomalously high feeding rates on large particles in fast flow were observed for *B. stolonifera.* The most likely explanation for this is a switch in feeding from mainly ciliary currents to feeding that involves a high degree of tentacular activity. Unfortunately, a switch in feeding technique was not anticipated and, consequently, lophophore behavior was not observed with a microscope during the experiments.

Furthermore, colonies were fixed and sampled when time permitted. When the feeding patterns were eventually discerned, there were no colonies available for observing lophophoral behavior (both species are highly seasonal in Florida). However, as mentioned earlier, laboratory observations indicate that feeding in many *Bugula* species does involve high degrees of tentacular activity and encagement (Winston, 1978). Only moderate levels of tentacular activity were observed in *B. stolonifera*, but since Winston's observations were made in still water and the sizes of suspended particles were unspecified, conditions that would have invoked high degrees of tentacular activity or encagement by *B. stolonifera* may not have been present.

The inferred switch in feeding mode by *Bugula stolonifera* is induced by increased flow rate and depends on particle size. The larger *B. neritina* showed no evidence of a switch in feeding behavior. However, if particles of larger size or perhaps if faster flow velocities had been employed, a switch in feeding would be expected. High degrees of tentacular activity were observed for *B. neritina*, including the formation of cages with its tentacles (Winston, 1978). The reduction in feeding on small and medium-sized particles with increased flow by *B. stolonifera* is in accord with previous results (Okamura, 1985).

Best and Thorpe (1983, 1986) provide evidence that bryozoans are capable of altering the strength of their feeding currents and do so in response to particle concentration. An alternate explanation for the present results is that the feeding patterns are produced by feeding currents of different strengths. If this is so, the greater flux of large particles in fast flow would induce *Bugula stolonifera*, but not *B. neritina*, to produce stronger feeding currents. While this is a possibility, it is considered unlikely since *B. stolonifera* fed disproportionately on large particles present in mixtures (composed of equal proportions of all three particle sizes) in fast flow (Okamura, in prep). In this case, if stronger feeding currents were produced, particles of all three sizes would be expected to be ingested in equal proportions. It is more likely that the disproportionate ingestion of large particles from mixtures was a result of selective tentacular feeding.

It is notable that the apparent switch in feeding by *Bugula stolonifera* entails such a large increase in capture. Tentacular feeding may involve a much greater energetic expenditure than ciliary feeding. Only when the gain is great (*i.e.*, many large particles per unit time) will feeding that involves a high degree of tentacular activity be a worthwhile strategy. Note that a switch to tentacular feeding results in a much greater amount of "biomass" captured [mean mass of large particles captured by *B. stolonifera* in fast flow = 30.80×19^{-9} g (SD = 8.50), of medium-sized particles = 6.21×10^{-9} g (SD = 1.87), and of small particles = 1.09×10^{-9} g (SD = 0.42)]. However, the costs of ciliary and tentacular feeding are unknown. The reduced surface area offered by small particles for tentacular contact may preclude tentacular feeding on particles below a minimum size, or perhaps particles must exceed a certain relative size to be perceived individually.

Plasticity in feeding behavior and its implications

It is evident that many suspension feeders are capable of great plasticity in feeding behavior. Alternate feeding techniques are invoked by variations in the suspension from which they capture their food. These variations may be characteristics of the prey items (*e.g.*, size, motility, chemistry) or physical properties of the medium itself (*e.g.*, temperature, density, and the patterns of fluid flow). Since suspension feeders will regularly encounter suspensions that vary in both physical properties and prey items, plasticity in feeding response is expected. The study of suspension feeding in still water on uniform particles may often provide an incomplete picture of the feeding of many organisms. This is exemplified by the studies of Best and Thorpe (1983, 1986). They argue that tentacular flicking and the more localized ciliary reversal mechanism that Strathmann (1982) proposes to account for particle capture during ciliary feeding are not the main methods of feeding employed by bryozoans. They suggest that, overall, the bulk of particles ingested are those that feeding currents carry down the center of the lophophore towards the mouth. The importance of ciliary reversal and tentacular activity in feeding are rejected on the basis of calculating the number of reversals and tentacular flicks required to explain the ingestion rates they observed. However, their evidence may be biased due to their use of extremely high particle concentrations (50–200 cells μl^{-1}), small particle sizes, and the absence of ambient currents in their experiments. Their study suggests that very high particle concentrations may swamp contributions to feeding by mechanisms other than the bulk flow of particles through the center of the lophophore, while this study suggests that high degrees of tentacular activity depend on both particle size and ambient flow.

Many investigators have studied the relationship between bryozoan colony form and the patterns of self-generated feeding currents through colonies (Cowen and Rider, 1972; McKinney, 1977, 1986a, b; Taylor, 1979; Anstey, 1981; McKinney *et al.*, 1986). Results reported here indicate that feeding currents may not always be of primary importance in particle capture. The potential for alternate feeding behaviors should be appreciated when interpreting colony morphology solely in terms of feeding current patterns. Both stenolaemate and gymnolaemate bryozoans display high degrees of tentacular activity even in still water (Winston, 1978). Tentacular feeding from faster ambient flow and/or on certain types of prey may provide a significant source of nutrition for a variety of bryozoans.

Optimal foraging theory attempts to explain and predict many aspects of the foraging behavior of animals by assessing foraging tactics in terms of maximizing net rates of energy gain and therefore fitness (*e.g.*, Schoener, 1971; Pyke 1977, 1984; Hughes, 1980). Which prey will be the "best" is determined by the energy content of the prey and the energetic cost to the predator of searching for and handling the prey. Thus, understanding patterns of prey selection, prey vulnerability, and feeding behaviors is crucial in the interpretation of foraging strategies. Particle size appears to relate to prey vulnerability in bryozoan feeding. Flow velocity induces a switch in feeding behavior that results in a shift in the size of particles captured. Furthermore, flow velocity appears to control the vulnerability of particles of certain size ranges even when feeding under one mode (note greater feeding on large particles in slow flow but on medium-sized particles in fast flow by *Bugula neritina*). Prey vulnerability and patterns of prey capture are thus determined by both the constraints imposed by flow and by the flow-induced change in feeding tactics. This suggests that the role of flow on particle size selection and the behavior of suspension feeders merits further investigation. In addition, a switch in feeding tactics by bryozoans implies that these organisms perceive and assess prey availability and subsequently adopt the most efficient feeding mode (*i.e.*, the one that maximizes net energy gain). It appears that predictions of optimal foraging theory may be applicable to benthic suspension feeders despite their seemingly simple sensory capabilities and sessile existence.

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